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THE COLORS OF NORTHERN MONOCOTYLEDONOUS FLOWERS.

JOHN H. LOVELL.

IN the accompanying table the 1058 species of northern monocotyledonous flowers recognized in the *Illustrated Flora of Britton and Brown* have been arranged according to their predominant colors. The territory covered extends from the Atlantic Ocean westward to the 102d meridian, and from the parallel of the southern boundary of Virginia and Kentucky northward, to include Labrador and Manitoba. The green or dull-colored flowers number 857, and the non-green 201, of which 41 are yellow, 82 white, 22 red, 22 purple, and 34 blue. Of the 28 families, 12 contain yellow flowers, 11 white, 5 red and purple, 5 blue, and 15 green. Six families are represented by only a single species. Yellow and white flowers usually occur in the same families, except in the Alismaceæ with 19 white, and the Xyridaceæ with 6 yellow species. There are described in the sixth edition of *Gray's Manual* 785 monocotyledons, which, for the purpose of comparison, I have also tabulated according to their colors; 621 have green or dull-colored flowers, and 164 non-green, divided into 38 yellow, 67 white, 19 red, 19 purple, and 21 blue. The yellow, red, and purple are less than those of the *Illustrated Flora* by 3 each, the white by 15, the blue by 13, and the green by 236. This difference is due partly to the more restricted area of the *Manual*, and partly to a different conception of varieties and species.

The flowers of the four families, Typhaceæ to Scheuchzeriaceæ, are either anemophilous as in Typha and Potamogeton, or hydrophilous as in Ruppia and Zostera, or self-fertilized as is probably the case in Triglochin and Scheuchzeria. The perianth segments are very small or wanting, and the numerous flowers are usually crowded in a greenish inconspicuous inflorescence which is often spathaceous. The spikes of Typha are, however, brown or black, and those of Potamogeton are frequently reddish. The 19 species of the Alismaceæ all have white petals and are attractive to Syrphidæ. On the small flowers of Alisma Plantago-aquatica, Müller collected 5 flies of this genus, and on Sagittaria latifolia I have taken 11 Syrphidæ, 6 other Diptera, 2 Coleoptera, and 4 bees. In the latter species the globular mass of yellow stamens, about 40 in number, are brought into strong relief by the white petals. The primitive color of the Alismaceæ was doubtless green, the transition of which to white may be illustrated by many examples. The involucre of Cornus changes from green to white during growth; the floral leaves of *Monarda clinopodia* are white; the calyx of Polygonum in different species is green, greenish-white, and white; the upper sepal of *Habenaria obtusata* is green with whitish margins; the perianth of *Ornithogalum umbellatum* is white above and green beneath; Chrosperma (Amianthium) is white, but turns greenish with age; I have observed the marginal neutral flowers of a culture variety of Hydrangea to remain upon the plant for many months and change from white to pale green, and many small flowers vary from green to white. Of the Vallisneriaceæ Philotria and Vallisneria have white hydrophilous flowers, and Hydrocharis is entomophilous. Müller regards Vallisneria as an intermediate stage between a water-fertilized and an insect-fertilized plant.

The Gramineæ with 371, and the Cyperaceæ with 334 species include nearly two-thirds of northern monocotyledons. The same external conditions appear to have been favorable to the development and continuance of a great number of forms in both families. The flowers are wind fertilized, though they are visited occasionally by flies, bees, and beetles for pollen. The perianth is nearly suppressed and is represented only by scales or bristles. Both the glumes of the Gramineæ and the bracts of the Cyperaceæ are often reddish or purplish. This coloration is of physiological importance, according to Pick and Stahl, and by converting light-rays into heat promotes both in young leaves and the organs of flowers transpiration, metabolism, and growth. Darwin states in "Variation in Animals and

Plants under Domestication" that red wheats and red sugar canes are more hardy than white, and I have also noticed that the most vigorous variety of maize or Indian corn in my garden had purplish-red culms, glumes, and silk. The red coloring of the styles is believed to favor the growth of the pollen tubes and occurs in many flowers. Leaf variegation is found in some grasses, as in Eulalia, one beautiful variety of which has the leaves striped longitudinally with white, and in another marked transversely with yellow.

Many Araceæ are cultivated for their handsome foliage, which is marbled or striped with yellow, white, purple, and red. The capability of the leaf to produce bright coloration has determined the adaptation of the spathe for attractive purposes, and its development has been attended by the reduction or suppression of the perianth. The spathe of *Arisæma triphyllum*, Indian turnip, is variegated with purplish and white stripes, and C. M. Weed found the flowers visited by small diptera of the genus Mycetophila, or family of fungus gnats. *Symplocarpus fœtidus*, the skunk cabbage, has the spathe spotted and striped with purple and yellowish-green; the odor is repulsive, and the visitors are small active flies of the genus Phora. *Calla palustris* has a conspicuous white spathe and, according to Eu. Warming, pond snails aid in the fertilization; Delpino mentions more than 4 European species of Araceæ, which, in his opinion, are fertilized by snails. In Orontium the perfect bright yellow flowers are densely crowded over the narrow spadix, and the green spathe is distant, investing only the lower part of the scape. The investigation of the numerous tropical species of this family promises to reveal many remarkable adaptations. The Lemnaceæ are regarded as simplified Araceæ, and the minute green flowers, in the opinion of Ludwig and Müller, are adapted to insects which live upon the surface of the water.

The small yellow flowers of the Xyridaceæ, which are regular, trimerous, and solitary in the axils of scale-like bracts, are evidently primitive in type, and are probably derived directly from ancestral green forms. This transition is illustrated in Hypoxis, which has the perianth segments yellow above, but the three outer green on the lower side; in *Nymphæa advena* the lower half of the outer sepals is green, and the upper half yellow; *Trollius laxus*, which grows in dense swamps, has greenish-yellow sepals, but the culture varieties are bright yellow, while the perianth of *Veratrum viride* is yellowish-green. Henslow thinks it probable that the yellow coloration of the petaloid structures is correlated with the yellow coloring of the anthers and pollens, universal among gymnosperms and very prevalent among angiosperms, and also extending to the anther scale of Pinus and the sporophylls of Lycopodium. Certainly yellow is the first color to be developed in many dicotyledonous families.

The 12 species of the Commelinaceæ all have blue flowers, except *Tradescantia rosea*, which is rose-colored, and the smallest northern species with narrow grass-like leaves and few flowers. Blue in this family appears to have been preceded by a reddish stage, and this view is strengthened when we remember that many blue Boraginaceæ have passed through a red stage, as Myosotis, Pulmonaria, and Echium, several species changing from red to blue during the course of individual development. The filaments of Tradescantia are bearded as in Verbascum, which is visited by pollen-collecting bees.

The original color of the Pontederiaceæ was almost certainly yellow, as it still is of the smallest species, *Heteranthera dubia*, water star grass, which has a slender stem and linear, sessile leaves. Every stage of the transition from yellow to blue is shown by *Viola tricolor*, and in Gentiana the simplest species, *G. lutea*, is yellow, but the more highly specialized species are purple-blue. The middle lobe of the upper lip of *Pontederia cordata* is marked by two yellow spots, which serve as honey guides. This is one of the handsomest as well as commonest of river plants, producing thousands of spikes of purple-blue flowers with blue anthers. The most important visitors are *Bombus vagans* and *B. borealis*, though I have also collected upon the flowers two other bees, four Lepidoptera, and four Diptera.

The Juncaceæ have a small, regular six-parted perianth which is often reddish or purplish brown. The flowers are anemophilous and proterogynous, though self-fertilization of open flowers and cleistogamy occur. Several European species have rather conspicuous flowers and attract insect visits.

The Melanthaceæ have regular, perfect, and, for the most part, small flowers in panicles and racemes. Many of the species grow in woodlands and swamps, secrete nectar in readily accessible positions, and are visited by Diptera, as in Tofieldia and Veratrum. The flowers exhibit but little bright coloring and are chiefly greenish-white or greenish-yellow; in Zygadenus and Melanthium there are green, greenish-yellow, and greenish-white species; in Veratrum yellowish-green and purplish. Yellow, white, and purple appear to have been developed directly from the primitive green without passing through any intermediate stage. There is a complete absence of red and blue and of variegation. The primitive color of this family and the two succeeding was undoubtedly green, resembling the wind-fertilized Juncaceæ, with which they are closely allied in structure.

The Liliaceæ have attained a much higher stage of coloration than the Melanthaceæ, and the inflorescence exhibits the most brilliant and variegated hues. The flowers are solitary or clustered, very large and conspicuous, and, in some instances, adapted to the visits of a single species of insect. They are very remarkable for their range of color and, long since, compelled botanists to lay aside the cyanic and xanthic speculations of de Candolle. The hyacinth displays every shade of yellow, white, red, and blue, and Darwin gives several instances of red and blue flowers produced on the same truss; the tulip exhibits yellow, white, red, and purple-violet; and many other genera are almost equally polychromatic. The 9 species of Allium are green, white, and rose, the development of coloring having proceeded in this order. The honey is abundant and is more accessible in the green and white species than in the rose; the inflorescence is umbelloid, and the guests are bees, Lepidoptera, and flies. Florists also offer bright yellow and blue forms. About 45 species of the genus Lilium are known, many of which are adapted to diurnal and nocturnal Lepidoptera. The entire genus is justly admired for the beauty of its flowers.

It has long been a favorite in floriculture and many varieties have been produced by hybridization. Seven species with yellow, orange-red, and scarlet flowers are indigenous to the northern states, and *L. tigrinus* is adventitious from Asia. Red flowers are peculiarly attractive to butterflies, and they are the chief agents in pollenizing many pinks and species of phlox, and, according to Müller, of Tritoma and the fiery red *L. bulbiferum*. I have repeatedly seen *L. Philadelphicum*, which is orange-red spotted with purple inside, visited by *Argynnis aphrodite*, the silver-winged butterfly, which is itself yellowish-red spotted with silver, but never by any other insect. The yellow nodding flowers of *L. Canadense* are visited only by bees, and I have seen *Bombus vagans* rest first upon the stigma and then climb the stamens to the base of the corolla. The white exotic species, such as *L. martagon* and *L. harrisi*, are sought by Sphingidæ or hawk moths. The genera Lilium and Tulipa excellently illustrate the transition from yellow to red, presenting every intermediate step, as yellow, orange, orange-red with a broad yellow band, orange-red, dark scarlet with yellow stripes, and fiery red. *Tritoma abraria* is coral red and, according to Gray, changes to orange and then to greenish-yellow.

Erythronium, Calorchortus, and Muscari are visited by bees, and display the most brilliant colors. The 4 native species of Erythronium are respectively yellow, white, rose, and lavender; and those of Muscari are blue and white, but under cultivation there are also yellow and red forms.

The genus Yucca is chiefly confined to Mexico and the southern states, but 3 species occur north of Tennessee. The flowers are large, white above and greenish beneath, and are pollinated at night by a white Teneid moth, *Pronuba yuccasella* A plant in bloom is a magnificent sight, the flower stalk sometimes, as in *Y. filifera* of Mexico, rising to the height of 50 feet and supporting a panicle 5 or 6 feet long. The manner of pollination is phenomenal in the extreme and has been thoroughly investigated by Riley and Trelease. The structure of the moth Pronuba is very abnormal among lepidopterous insects, as it is provided with tentacles for collecting pollen and an ovipositor for puncturing the yucca pods. In the evening this small moth climbs in succession half a dozen stamens, and collects the pollinia in a compact ball beneath its head; it then punctures the pod and deposits its eggs among the ovules, after which, in order that the growing seed pods may afford food for the young larvæ, it deliberately climbs the short style, and intentionally rubs the pollen with its tentacles upon the viscid stigma. As the stamens are shorter than the pistil the plant would not produce seed unless fertilized by Pronuba.

The Convallariaceæ commonly grow in moist woods and thickets, and have dull-colored, rather inconspicuous flowers. Of the 23 species 2 are greenish-yellow, 11 white, 1 rose-purple, 4 purple, and 5 green; there are no bright red or blue flowers, and none adapted to Lepidoptera. The most frequent visitors are bees and flies. The greenish flowers of Asparagus are mellifluous, pleasantly scented, and mellitophilous. The male flowers are twice the length of the female, and in consequence of their increased conspicuousness are visited first by bees. On the greenish-yellow flowers of *Clintonia borealis* I have collected the honey-bee, *Bombus consimilis*, and small beetles, *Anthobium pothos*, feeding on the pollen. The short, white, bell-shaped flowers of Convallaria are open to all bees, but the longer tubular blossoms of Polygonatum only to bumblebees. The largest genus is Trillium with 8 species; 3 white, 4 purple, and 1 greenish. The purple-flowered species have been derived, apparently, directly from the primitive green, for *T. viride* is light green or purplish-green, *T. erectum* is purple, sometimes greenish, and *T. sessile* is purple or green. A white variety of *T. erectum* is common, especially in New York, the specimens of which in my herbarium are smaller than the purple form. C. M. Weed saw the flesh fly, *Lucilia cornicina*, on the flowers of this species, which has a disagreeable odor, and I have also seen minute Diptera. Several species are pleasantly odorous and are probably visited by small bees. The Smilaceæ have small, regular, diœcious, greenish flowers attractive to Diptera.

The Amaryllidaceæ are principally a tropical family, only

1 species, *Hypoxis hirsuta*, star grass, being found in New England. The flowers are often white, sweet-scented, and attractive to night-flying Lepidoptera. Of the 6 northern species, 3 are yellow and 3 white. The coloration of the exotic species is unsurpassed in beauty and magnificence, orange, white, red, and crimson predominating.

In the Iridaceæ, on the contrary, blue, violet, purple, and yellow are the more common colors, often variegated and gaudily spotted. The flowers of Iris are adapted to the larger bees, though the bright yellow *I. pseudacorus*, naturalized from Europe, has been seen both there and in New England to be frequently visited by a syrphid fly of the genus Rhingia. On *I. versicolor* I have taken four different bees; the honey-bee often passes in and out sideways between the perianth segment and the petaloid style without effecting fertilization, and *Halictus similis*, also common, I have observed breaking open immature anthers for the pollen. Yellow markings, yellow flowers, and reversion to yellow are of frequent occurrence, especially in Iris and the familiar Gladiolus and Crocus, and point to this color as belonging to an earlier stage of this family.

At the head of the monocotyledons stand the magnificent and extensive family of the Orchidaceæ, which, according to Engler, has no possible connecting link with the liliaceous families. The flowers are zygomorphous in a very high degree and possess marvelous adaptations for fertilization by insects, which have been very fully described, but can only be properly understood by the examination of living specimens. Of the 61 northern species, 10 are yellow, 18 white, 8 red, 14 purple, and 11 green. The number of white and green flowers appear surprisingly large until it is observed how sparingly our indigenous species are visited by insects. There are no blue flowers, and this is an unusual color among orchids, though found in the pale blue *Vanda cærulæ* of India. There is much variegation, and reversion to white of the pink-purple forms is common as in *Habenaria grandiflora* and *Pogonia ophioglossoides*. Many of the large pink-purple or rose-colored flowers are attractive to bumblebees. *Orchis spectabilis* blooms in early springtime and is visited only by female forms of Bombus, which are then alone on the wing; during two years I have repeatedly examined many blossoms of the handsome *Pogonia ophioglossoides*, but have collected only a single specimen of *Bombus consimilis*. The white flowers of Gyrostachys (Spiranthes) and Peramium (Goodyera) are also occasionally visited by bumblebees. The genus Habenaria is adapted to Lepidoptera, the white and yellowish species, which are often sweet-scented, being pollinated by crepuscular or nocturnal moths. In some instances I have found the grayish hairs of these insects adhering to glutinous surfaces. The fertilization of some 10 species has been described by Asa Gray. Small purplish or green flowers are visited by small Hymenoptera and Diptera or are self-fertilized. On the purplish and greenish inflorescence of Listera, twayblade, Darwin collected in England small Hymenoptera and Diptera, and on the extremely small and inconspicuous but odorous flowers of *Herminium mornorchis* George Darwin collected 27 specimens of minute Hymenoptera, Diptera, and Coleoptera, the largest being less than $\frac{1}{20}$ of an inch in length. The small green flowers of *Habenaria hyperborea* and *Epipactis viridiflora* are self-fertilized. Scentless plain green flowers of a species of Epidendrum in South Brazil, according to Fritz Müller, freely secrete honey and attract insects.

A simpler and earlier stage of the Orchidaceæ has been partly preserved in Cypripedium, the floral organs of which are less modified than those of other genera. An enormous amount of extinction, Darwin believes, has swept away the intermediate forms. The flowers are visited with extreme rarity by Andrenidæ, while species of Bombus are liable to be held captive and perish miserably of starvation. Of the 6 species in the northern states, 2 are yellow, marked with purple, 2 white striped with purple, and 2 red and white. As the lip is evidently the chief object of attraction the other perianth segments are dull colored, green, brown, white, or purple.

The Orchidaceæ are remarkable for the variety of colors, often three or four, presented by individual flowers; in a species of Dendrobium from India the sepals and petals are white, tipped with purple, and the lip is bright orange with two crimson spots. This is probably due to the marked tendency of the species to variation, as described by Müller and others, and to which they attribute the multiplicity of forms of flowers. The high degree of zygomorphy and bright coloration have evidently been produced by the agency of insects, since the lip, the petal most modified in form and color, is the segment most visited, while the other segments of the perianth often retain their primitive form and plain green coloring. Insects have not, however, been able to induce particular colors, but their work has been the fixation by selection of those naturally produced by the flowers. This is well shown by the rarity of blue among the Orchidaceæ. This color is very attractive to bees, yet its development has not necessarily followed the high specialization of the flowers in response to their visits. Its presence or absence is rather dependent upon the chemical constitution of the nutritive fluids or other internal conditions. There may even be no bright coloring, as in the mellifluous plain green species of Epidendrum mentioned above.

The monocotyledonous families were probably very early differentiated, and their subsequent development has proceeded along parallel lines, but without any connection with each other. With few exceptions, the families possess a perianth, though it is frequently rudimentary, and in the majority of species non-petaloid. In the opinion of Engler the floral envelopes have not been induced by insect pollination. Their very general occurrence points to their early development, and their first office was undoubtedly protective in its nature, similar to that performed by the scales of the gymnosperms. In anemophilous families the perianth has remained unmodified or, where the protective office has been assumed by glumes or bracts, as in the Gramineæ, has nearly disappeared; while in the entomophilous families insect pollination has caused it to be enlarged and specialized. When the expenditure of producing petals, nectar, and color is considered, as well as the vast number of individuals blooming at a time when they would be brought into competition with many entomophilous flowers, it cannot be doubted that the Gramineæ and Cyperaceæ are more efficiently pollinated by the wind than could possibly be the case by the existing number of insects.

SUMMARY.

1. The primitive color of the perianth of the monocotyledonous families was green, as it still is in the greater part of the species which are anemophilous or self-fertilized. A few of the oldest families, with an indefinite number of stamens and carpels spirally arranged, have probably never possessed floral envelopes.

2. Yellow, white, and lurid, or greenish-purple flowers have in numerous instances been derived directly from the primitive green; red flowers have passed through a yellow or white stage; and blue and purple-blue have been derived from yellow, white, or red forms. Reversion to white is most common, but reversion to red or yellow also occurs.

3. Physiological conditions appear to have often played an important part in determining the coloration of the petals, while "insects have contributed to the fixation of such characters when once acquired."

4. In general, among monocotyledons yellow flowers are visited by bees and flies; white flowers, by bees, nocturnal Lepidoptera, flies, and beetles; lurid-purple, by flesh flies; red, by bees and butterflies; and blue, chiefly by bees. Red and blue flowers usually have the honey concealed, which is a far more effective cause of the limitation of insect visits than color.

When the honey is abundant and exposed, and the flower pleasantly odorous, it may prove attractive to any anthophilous insect. In proof of this it may be stated that insects frequently attempt to visit flowers from which they are excluded. I have seen butterflies standing beneath the perianth of *Iris versicolor* and stealing the honey, without rendering any service in return; an hymenopter, probably an ichneumon fly, was observed, but not caught, examining the center of the flower for nectar, and of course, unsuccessfully; flies are attracted by the bright colors of *Impatiens biflora* to the outside of the calycine sac, and I have often seen *Philanthus solivagus* flying from flower to flower of *Chelone glabra* and examining the lips for nectar, but never entering the corolla.

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ORDERS.	FAMILIES.	YELLOW.	WHITE.	RED.	PURPLE.	BLUE.	GREEN OR DULL COLOR.	TOTAL.
Pandanales. .	Typhaceæ . . .						2	2
	Sparganiaceæ .						4	4
Naiadales . .	Naiadaceæ . .						42	42
	Scheuchzeriaceæ		1				3	4
	Alismaceæ . .		19					19
	Vallisneriaceæ .		3					3
Graminales. .	Gramineæ . . .						371	371
	Cyperaceæ . .						334	334
Arales . . .	Araceæ	1	2				5	8
	Lemnaceæ . .						11	11
Xyridales . .	Mayacaceæ . .		1					1
	Xyridaceæ . .	6						6
	Eriocaulaceæ . .						5	5
	Bromeliaceæ . .	1						1
	Commelinaceæ .			1		11		12
	Pontederiaceæ .	1	1			2		4
Liliales .	Juncaceæ . . .						47	47
	Melanthaceæ. .	7	10		2		5	24
	Liliaceæ . . .	6	13	11	1	6	1	38
	Convallariaceæ .	2	11	1	4		5	23
	Smilaceæ . . .						11	11
	Hæmodoraceæ .	1						1
	Amaryllidaceæ .	3	3					6
	Dioscoreaceæ .	1						1
	Iridaceæ . . .	2		1				17
Scitaminales .	Marantaceæ . .				1	14		1
Orchidales . .	Burmanniaceæ .					1		1
	Orchidaceæ . .	10	18	8	14		11	61
	Total . . .	41	82	22	22	34	857	1058